Pak. J. Bot., 43(5): 2519-2525, 2011.

PHYSICAL AND GENETIC ANALYSIS OF *Ph1* GENE REGION ON THE LONG ARM OF CHROMOSOME 5B IN WHEAT AND RELATED CEREALS

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Abstract

Genetic activity of *Ph1* (pairing homoeologous) gene on the long arm of chromosome 5B, blocks chromosome pairing during meiosis in related genomes thus hindering the improvement in wheat on one hand but guaranteeing stability of the genome during its evolution on the other hand. Efforts have been made to clone this gene; however, complex nature of the wheat genome and low density of markers in the region may have been the prime reasons for no or low success in cloning this important gene. We aimed to enrich *Ph1* gene region by identifying more markers through comparative mapping approaches. Twenty nine genetic linkage and 12 physical maps in *Triticeae* (oat, rice, rye, sugarcane, wheat, and barley) were used for comparative mapping. Thirteen anchored markers that were previously mapped in the *Ph1* gene region were used to identify additional markers in and around the *Ph1* gene region across *Triticeae*. Consensus physical and genetic linkage maps were generated in wheat and related species for the region. Using comparative mapping approaches, a total of 76 markers were identified in a rather larger gene rich region (GRR) '5L0.5' that contains the *Ph1* gene region. Of these 76 fifty six (56) were putatively mapped in 5L0.5 GRR whereas 33 were mapped in the *Ph1* gene region. By comparing individual consensus physical and genetic linkage maps it was observed that the region is conserved among *Triticeae* and *Poaceae* from a poor to fairly high density. Saturation mapping in the *Ph1* gene region will lead to eventually clone the gene which will have greater impact in biological processes of life systems.

Introduction

Wheat (*Triticum aestivum* L.) is one of the world's most important food crops, belonging to the family *Poaceae*, tribe *Triticeae*, comprising some 300 species classified into 22 genera (Love, 1984) including several other cereal crop species such as barley, rye and triticale.

World demand for wheat is growing at a much greater rate per year than genetic gains in yield potential. This warrant to pay immense attention for wheat improvement in order to meet the needs of rapidly growing population especially in the developing world. For this purpose both the conventional and modern scientific techniques need to be exploited. A major impediment to such efforts is the lack of chromosome pairing in related genomes during meiosis thus raising barriers in shuffling the genes between wheat and its relatives. Wheat having three related genomes A, B and D derived from its wild progenitors appeared to be as allohexaploid. The corresponding chromosomes can compensate for each other's absence or addition as the three genomes are closely related (Sears *et al.*, 1966). The pairing affinity among these chromosomes is suppressed mainly by the genetic activity of the "pairing homoeologous" gene, *Ph1* which is present on the long arm of chromosome 5B (Sears & Okamoto, 1958). *Ph1* gene suppresses the pairing of homoeologous chromosomes and allows only regular pairing between homologous chromosomes. This type of arrangement may be manifested by the presence of only bivalents at meiosis. Furthermore, the *Ph1* locus also prevent homoeologous chromosome pairing between wheat and several other related genomes in hybrids (Riley *et al.*, 1959; Jauhar & Chibbar, 1999**).** On one hand *Ph1* gene plays an important role in maintaining the integrity of the wheat over millions of years of evolution but on the other hand, it is a greater impediment to transfer the genes from the related gene pool into wheat imposing even bigger challenges to wheat improvement.

Mutant lines *Ph1*b and *Ph1*c were generated in wheat using X-ray irradiation (Sears, 1977; Giorgi & Barbera, 1981) *Ph1b* is present in hexaploid wheat (*Triticum aestivum*) cultivar Chinese spring, whereas mutant *Ph1*c is in tetraploid wheat (*Triticum turgidum*) cultivar Cappelli CPP (dup.*Ph1*) with a duplicated interstitial region encompassing the *Ph1* gene is also available (Dvorak *et al.*, 1984). Following the molecular genetic characterization of the *Ph1* locus, five additional deletion mutants covering the region were identified (Sears, 1977; Roberts, 1989). In addition, bacterial artificial chromosomes (BACs) were sequenced and analyzed to elucidate the complexity of this locus (Altschul *et al.*, 1997; Ewing & Green, 1998). It is important to identify the conserved regions in other related genomes which require comparative genome analysis and enrichment of the region in wheat genome. It was also aimed to identify closely linked molecular markers in order to score the gene.

Methodology

Comparative mapping in the region: Using comparative mapping approaches across *Triticeae*; the most potential markers for the region were identified as anchored markers. The marker(s) mapped precisely within the region were used to find closely linked markers in the physical or genetic linkage maps. The information was obtained from graingenes database (http://wheat.pw.usda.gov/GG2/index.shtml), published articles, reviews, relevant books and internet sources. Though the criteria were relaxed, a stringent threshold was established by considering two decisive flanking markers on either side of the region. The markers thus identified were placed within the flanking markers and were considered as anchored markers which can be used in any future study.

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Construction of consensus genetic linkage map of the region: The consensus genetic linkage map of the region was developed by combining the data from genetic linkage maps for group 5 chromosomes and for the 5L0.5 region that contain *Ph1* locus. The map was developed by manual alignment of the common markers to each individual map and then superimposing the markers that were unique to each map, described by (Shah & Gill, 2000; Shah & Gill, 2001; Shah & Hassan, 2005; Khan & Shah, 2009). The marker loci common between two maps were used as anchor markers, and the genetic distances for loci between anchor markers were extrapolated. Genetic distances used for the construction of a consensus genetic linkage map are relative rather than absolute. The distances between markers were slightly variable on different genetic linkage maps; therefore, an approximate estimate of the genetic distance is given (Erayman *et al*., 2004; Shah & Hassan, 2005). The consensus genetic linkage maps for each species i.e., wheat, barley, oat, rye and sugarcane (Heun *et al*., 1991; Boyko *et al.,* 1999) were constructed which then were used to generate a combined consensus genetic linkage map for the region among the whole *Triticeae*.

Construction of consensus physical map of the region: Anchored markers were used for the generation of physical consensus map of 5L0.5 gene rich region containing *Ph1* locus. A strategy described by (Shah & Hassan, 2005) was adopted to generate consensus physical map of the region. The map was constructed using physical mapping data from published map (Gill *et al*., 1993; Gill & Gill, 1996; Faris *et al*., 2000; Shah & Gill, 2000; Shah & Gill, 2001; Erayman *et al*., 2004). A skeleton map was drawn according to the average length of idiograms of homoeologous group5 chromosomes using information from Gill *et al*., (1991) and the URL: http://www.ksu.edu/wgrc/Germplasm/Deletions/grp5.html . The location of each marker locus was carefully checked on the individual homoeologues and was placed onto the shortest possible fraction length (FL) on the consensus physical map to mark and bracket the location of 5L0.5 region. This approach was adopted in the assumption that the region was conserved in a similar sized location among all the three genomes, but may not be resolved in any one or two of the individual genomes due to unavailability of deletion break points in that region (Shah & Hassan, 2005). The relative order of marker loci on all three homoeologues was also carefully considered when placing them on to the consensus physical map.

A comparative mapping approach was utilized across *Triticeae* to map potential genes and gene products in the region. Both the combined consensus genetic linkage and physical maps were placed side by side for comparisons and the potential locations of common markers were marked by line drawings. The physical and genetic distances were compared by visual observation.

Results and Discussion

By comparative mapping approaches 13 marker loci were identified specifically for the *Ph1* gene region that were previously mapped by researchers in or around this region across *Triticeae* species (Gill *et al.,* 1993; Gill & Gill, 1996; Faris *et al.,* 2000; Shah & Gill, 2000; Erayman *et al.,* 2004). The marker loci include cdo412a, bcd1949, cdo1090, cdo412b, mwg592, wg564, bcd1088, cdo786a, ksuS1, ksu8a, ksu8b and ksu8c all of which are RFLP clones representing expressed (cDNA) and or non-expressed (genomic) portion of the cereal genomes. By expanding comparative genomic analyses and utilizing the anchored markers a total of 146 markers were identified that were thought to be as the candidate loci for 5L0.5 GRR and or *Ph1* gene region. After a rigorous synthesis 76 putative markers (Table 1, Fig. 1b) were identified potentially for 5L0.5 GRR (within and around the region). The GRR 5L0.5 which is rather a larger region was previously marked by molecular marker analyses (Gill & Gill, 1996; Shah & Gill, 2000; Erayman *et al.,* 2004) on the chromosome 5BL of wheat that contains the *Ph1* gene region. Majority of these 76 markers are RFLP clones (cDNA or gDNA) and were previously mapped in the *Triticeae*. Of these 76, 56 markers were mapped specifically to 5L 0.5 GRR between break points 5BL-1 and 5BL-11 between fraction length 0.55-0.59. Twelve markers were identified to be present in the distal region from 5BL-11 whereas 8 were present proximal from 5BL-1 end of the 5L0.5 region. Of the 56 markers identified for 5L0.5GRR, 33 were mapped in the *Ph1* gene region including 13 anchored markers that were previously mapped in the same region. The remaining 23 were present distal from the distal breakpoint of *Ph1* gene region.

Using a number of available literature sources such as internet, research articles, reports and book chapters (Dvorak *et al*., 1984; Gill *et al*., 1991; Anderson *et al*., 1992; Gill *et al*., 1993; Galiba *et al.*, 1995; Van Deynze *et al.*, 1995; Marino *et al.*, 1996; Blanco *et al.*, 1998; Röder *et al.*, 1998; Faris *et al*., 2000; Jin *et al.*, 2000; Spielmeyer *et al.*, 2000; Masojc *et al.*, 2001; Choi *et al.*, 2002; Paillard *et al.*, 2003; Elouafi & Nachi, 2004; Wight *et al.*, 2004; Rostoks *et al.*, 2005; Rodriguez *et al*., 2006; Wenzl *et al.*, 2006; Varshney *et al.*, 2007) we developed consensus genetic linkage and physical maps for the region. We utilized more than 40 genetic linkage maps and 20 physical maps from across the *Triticeae* and *Poaceae*. The maps were selected on the basis of common markers present in *Ph1* gene region. First, individual consensus genetic maps in wheat, barley, oat, rye and sugarcane were generated separately using common flanking markers in each species for the 5L0.5 GRR that contains the *Ph1* gene region. A combined consensus genetic linkage map was generated by using all markers of individual consensus genetic linkage mps generated in wheat, barley, oat, rye and sugarcane, containing a total of 146 markers that were considered as potential candidates for the 5L0.5 GRR and or *Ph1* gene region. More or less the same criteria and procedure was adopted for the development of individual and combined physical maps in wheat and or *Triticeae*. A detailed comparison was made between consensus genetic and physical maps to see the distribution and conservation of *Ph1* gene region in the *Triticeae* genome. The results showed that the region is conserved among *Triticeae* and *Poaceae* family.

Table 1. Markers linked to *Ph1* gene region on chromosome 5BL between deletion point's 5BL-1 and 5BL-11 of wheat and on genomes of other cereals.

No.	Locus/marker name	Marker type	Chromosomal location in wheat	FL Distance	Deletion point	Location in other genomes
1.	ksuS1	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.aestivum*-4D, 5DL
2.	ksu8a	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
3.	ksu8b	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
4.	ksu8c	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
5.	tag614	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
6.	wg530	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley - 5H
7.	bcd351	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Wheat-5B Barley 1H, 5H
8.	ksuG44b	cDNA	5BL	0.55-0.59	5BL1-5BL11	Barley-5D, 5B, 5DL
9.	mwg522	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H Wheat 5A
10.	cdo385	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Sugarcane- 5B. Oat -5A,
11.	mwg805	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley-5H
12.	abc168	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley - 5HL.
13.	mgb10	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
14.	mbg63	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T. turgidum* -5AL
15.	mgb174	RFLP	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
16.	mgb191	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.turgidum*-5AS
17.	mgb301	RFLP	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
18.	mgb341	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.turgidum*-5AS
19.	ubp25	RFLP	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
20.	abc307	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.aestivum*-2BL
21.	ksuQ60	RFLP	5BL	0.55-.059	5BL-1-5BL-11	Not Known
22.	gwm499	SSR	5BL	0.55-0.59	5BL-1-5BL-11	Wheat (CS) Del-5B
23.	gwm371	SSR	5BL	0.55-0.59	5BL-1-5BL-11	Wheat (CS) Del-5B
24.	ksuQ10	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
25.	wg564a	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley-5HL, *T.aestivum*-5A
26.	mwg592	RFLP	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5HL
27.	abc302	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.turgidum*- 5AS
28.	bcd1088	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Oat -5A 5B, 5DL
29.	psr128	cDNA-STS	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H, *T.aestivum* 5B
30.	psr574	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	T.aestivum -5A,5B
31.	wg564b	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H, T.aestivum- 5A
32.	mwg956	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley-5H
33.	cdo412b	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Oat-5A, 5B, 5D
34.	cdo412a	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Oat-5A, 5B, 5D
35.	cdo1090	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Oat-2A
36.	cdo786a	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.aestivum* - 5A,5B
37.	bcd1949	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Wheat (CS) Del- 5B

Table 1. (Cont'd.).

No.	Locus/marker name	Marker type	Chromosomal location in wheat	FL Distance	Deletion point	Location in other genomes
38.	abc168a	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
39.	abc717	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
40.	abg387a	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -2H
41.	abg069	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
42.	bcd351a	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
43.	mwg2237	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
44.	mwg52a	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
45.	mwg583	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
46.	mwg768	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
47.	mwg923	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H, 2H
48.	bcd351b	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -1H, 4H
49.	cdo786c	cDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
50.	cdo1192	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
51.	fba127	gDNa	5BL	0.55-0.59	5BL-1-5BL-11	*T.aestivum* -5B
52.	wg364	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
53.	ksuQ35	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Not Known
54.	mwg52b	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	*T.* turgidum -5A
55.	abg314	gDNA	5BL	0.55-0.59	5BL-1-5BL-11	Barley -5H
56.	Large 4	gDNA-clone	5BL	0.55-0.59	5BL-1-5BL-11	*T.aestivum* -5B
57.	abg387b	gDNA	5BL	0.55-0.59	Distal to 5L.5	Barley -2H
58.	abg55	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
59.	cdo348b	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
60.	fba127b	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	*T.aestivum* -5B
61.	psb85	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	*T.aestivum* -5B
62.	bcd307	cDNA	5BL	0.55-0.59	Distal to 5L.5 region	*T.aestivum* -5B
63.	cdo388b	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
64.	wg1026	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Barely-5H
65.	bcd508	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
66.	fbb121b	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
67.	mwg2121	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
68.	mwg914	gDNA	5BL	0.55-0.59	Distal to 5L.5 region	Not Known
69.	cdo348a	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
70.	cdo388a	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
71.	cdo786b	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
72.	fbb121a	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
73.	fbb156	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
74.	ksuA1	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
75.	ksuD42b	gDNA	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known
76.	mwg624	gDNa	5BL	0.55-0.59	Proximal to 5L.5 region	Not Known

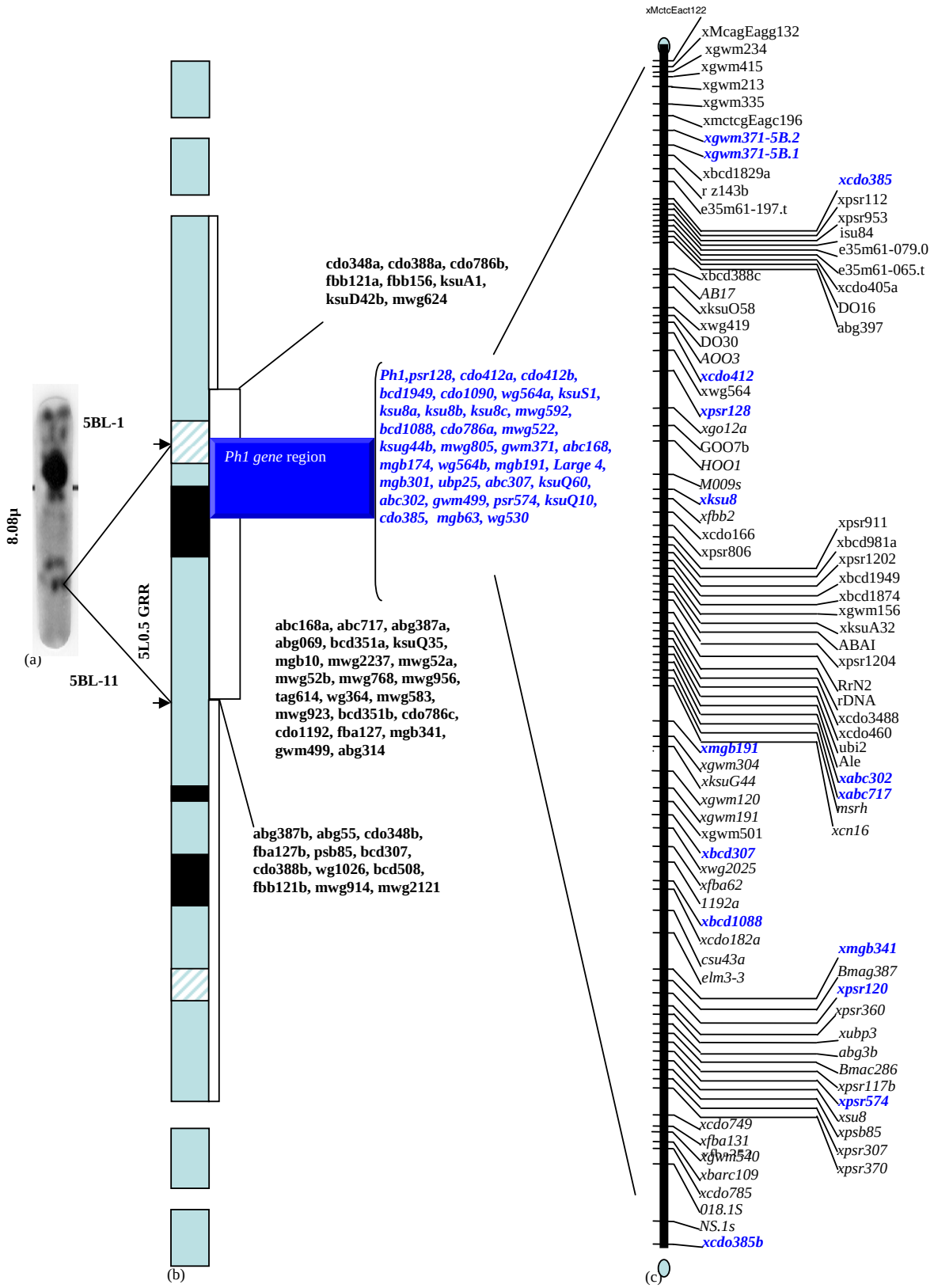

Fig. 1 Comparison of consensus physical and genetic linkage maps in *Triticeae*
(a). C banded karyotype of the wheat chromosome 5BL (b). Physical map of the 5L 0.5 gene rich region containing *Ph1* gene region (c). Consensus genetic linkage map across *Triticeae*. Blue and italic are *Ph1* region's markers.

Major crop plants including wheat, maize, barley, oat, and rice belongs to the grass family *Poaceae* of the tribe *Triticeae* that contains more than 15 genera and 300 species. It is now well documented that genes in cereals are present in clusters and the gene order and synteny are highly to moderately conserved among the species of *Triticeae* (Feuillet & Keller, 1999; Faris *et al*., 2000; Sandhu *et al*., 2001; Sandhu & Gill, 2002; Shah & Hassan, 2005) respectively. At current there are innumerable DNA markers present on one or more of the *Triticeae* genetic maps (GrainGenes data base, Barley database, RiceGenes, Oryzabase, Maizedata bases (DB)). Since majority of these markers are RFLP clones, thus may be used across the family; comparative mapping can be a very powerful approach for targeted mapping of any chromosomal region of interest. In current study, using comparative mapping approaches we identified 56 putative markers for '5L0.5 region' of which 43% (33/76) were mapped in the targeted *Ph1* gene region. Among remaining, 26% were mapped outside the target region, while the rest were previously localized to the proximal and distal gene clusters on 5BL of wheat (Gill *et al*., 1996a; Faris *et al*., 2000; Sandhu & Gill, 2002).

In conclusion, the comparative mapping based enrichment of a gene-rich region with markers is a powerful technique. Comparative mapping combined with targeted physical mapping strategy physically may localize potential markers and genes to the gene rich regions as was the case in '5L0.5GRR' in current study. The marker density can be increased for this region which will be useful for future contiguous map development and gene cloning. The markers for the *Ph1* gene region were found to be adequate to develop a contig for the region after further confirmation in the international databases and physically mapping on the *Ph1* gene deletion lines. The saturation of the region is from a poor to fairly dense in the cereal genome. High density mapping in the *Ph1* gene region will lead to eventually clone the gene which will have greater impact in biological processes and improvement of wheat crop for higher yield and resistance against biotic and abiotic stresses.

Acknowledgement

This study was completed as part of a research grant (NRPU Project # 20-634) awarded by Higher Education Commission (HEC) of Pakistan to Dr. M. Maroof Shah under National Research Program for Universities (NRPU).

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(Received for publication 24 July 2009)